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EFFECT OF IRRIGATION ON SURVIVAL OF THIRD-STAGE *HAEMONCHUS CONTORTUS* LARVAE (NEMATODA: TRICHOSTRONGYLIDAE)[1]

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ABSTRACT.— During May through October 1976, samples of sheep pellets containing laboratory-reared, third-stage *Haemonchus contortus* larvae were placed on irrigated and nonirrigated pasture plots at Provo, Utah. Periodically thereafter, grass clippings, soil scrapings, and remaining pellets were collected and baermannized to determine their comparative survival from the two environments. Water was added to the irrigated plots in accordance with a weekly sprinkling regime designed to furnish sufficient moisture to maintain pasture grass in this semiarid region. Meteorologic measurements were collected daily from both irrigated and nonirrigated sections. During the year the nonirrigated section received a total of 131 mm of precipitation, whereas an additional 979 mm of water were added via sprinkling to the irrigated section. The monthly mean maximum temperature at soil surface under grass cover for the six-month study period on the irrigated section averaged 17.7 C less than on the nonirrigated section, and the corresponding soil moisture content remained 14.4 percent higher. A bioclimatograph of conditions on the nonirrigated section showed that none of the months during the year had levels of temperature and moisture which fell within the prescribed limits for optimum pasture transmission of *H. contortus*; on the irrigated section only October of the six-month study period failed to have suitable conditions for optimum pasture transmission. Larvae placed on the plots survived significantly longer and also in significantly greater numbers on the irrigated section, and irrigation enhanced the ability of larvae to migrate from pellets onto vegetation.

Irrigation is the single most important process which permits the maximum utilization of agricultural lands in semiarid regions of the western United States. Approximately 18.8 percent of all agricultural land in the United States is irrigated (Irrigation Handbook and Directory 1972), and in the state of Utah that figure approximates 63 percent (Utah Agricultural Statistics 1976). In contrast to the marked beneficial effect of irrigation throughout the world, waste water from poor irrigational practices creates suitable breeding grounds for arthropod and molluscan vectors of disease agents (Surtees 1970, World Health Organization 1950). Irrigation in semiarid regions also creates favorable microenvironments for free-living stages of helminth parasites. Stewart and Douglas (1938) stated that irrigation water and transpiration of green vegetation in pastures in central California protected the developmental stages of nematode parasites in sheep from otherwise high temperatures. Furman (1944) reported increased populations of parasitic nematodes of sheep in an irrigated region of Sacramento Valley, California. Honess and Bergstrom (1966) reported increased nematodes in cattle that grazed on irrigated pastures in Wyoming. In central Utah from 68 to 71 percent of all cattle (Fox et al. 1970) and from 90 to 96 percent of all sheep (Wright and Andersen 1972) raised on irrigated pastures harbored parasitic nematodes of at least one species.

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The study herein reported was designed to determine the effect of irrigation on the survival of infective *Haemonchus contortus* larvae on experimental pasture plots in central Utah.

Materials and Methods

A 10 by 30 m fenced plot covered with Kentucky bluegrass (*Poa pratensis*) was established in Provo, Utah, and divided into irrigated and nonirrigated sections. Each section was further divided into rows of 14 plots, each 50 cm square and delineated as described by Andersen et al. (1970). Grass cover was mowed each week to an approximate height of 7 cm to simulate natural grazing conditions. Meteorological measurements from both irrigated and nonirrigated sections were monitored through instrumentation and procedures described by Andersen et al. (1974) and tabulated by computer programs described by Andersen and Roper (1975).

To secure infective larvae for the experiments, a sheep was given orally 12,000 third-stage *H. contortus* larvae. After the infection was patent, fecal pellets containing unembryonated eggs were collected from the sheep and incubated in the laboratory at 23 to 24 C and 100 percent relative humidity (RH) for one week until third-stage larvae developed. After incubation the pellets were divided into 30 samples of 40 grams each. Two samples were retained as controls in the laboratory to determine the average number of larvae which could be recovered following baermannization. The remaining 28 samples were distributed on the plots. One sample was placed in the grass on each of the 14 plots along one row of the irrigated section and one row of the nonirrigated section.

Experiments were started each Monday from May through October, which is the time period generally corresponding to the irrigation schedule used in Utah. For the first four days and weekly thereafter, grass clippings, soil scrapings, and remaining pellets were collected from each plot where fecal pellets containing infective larvae had been placed. Each sample was baermannized separately, and free-living nematodes in the recovered material were killed through the addition of HCl (Shorb 1937). The percentage recovery of larvae from each plot and each time interval was determined by dividing the average number of larvae recovered from the two control samples into the total number of larvae recovered from the grass, soil, and pellets.

Irrigation was performed each week from May through October by an oscillating sprinkler. The total depth of water (in mm)

TABLE 1. Relationship of meteorological conditions to survival of *Haemonchus contortus* third-stage larvae on irrigated and nonirrigated pasture plots, Provo, Utah, 1976.

	Temperature °C												
		Irrigated						Nonirrigated					
	Weather shelter	Soil surface under 7–10 cm grass cover			Soil surface bare ground			Soil surface under 7–10 cm grass cover			Soil surface bare ground		
Month	(Mean)	(Max.	Min.	Mean)	(Max.	Min.	Mean)	(Max.	Min.	Mean)	(Max.	Min.	Mean)
Jan	–3.4	–0.8	–1.8	–1.3	1.8	–1.6	0.1	0.7	–1.4	–0.3	2.7	–2.1	0.3
Feb	1.7	1.1	–0.9	0.1	9.6	–1.0	4.3	6.3	0.1	3.2	12.0	–1.7	5.2
Mar	2.1	7.4	0.9	4.1	22.2	0.7	11.5	14.0	0.6	2.3	25.9	–1.7	12.1
Apr	8.6	14.9	5.2	10.0	33.4	3.2	18.3	20.4	6.1	13.3	39.2	3.1	21.2
May	15.8	25.2	12.3	18.8	42.1	9.2	25.7	36.6	12.4	24.5	55.2	9.1	32.1
Jun	16.2	25.4	13.6	19.5	44.9	10.7	27.8	40.4	14.1	27.2	54.9	10.0	32.5
Jul	21.2	31.0	18.3	24.7	50.6	15.8	33.2	51.7	18.9	35.3	63.2	16.0	39.6
Aug	19.0	26.7	16.8	21.8	42.3	13.7	28.0	52.1	16.1	34.1	60.8	13.3	37.1
Sep	16.8	24.6	13.9	19.2	46.6	12.3	29.5	45.7	13.6	26.7	52.1	11.7	31.9
Oct	8.5	16.0	6.4	9.7	25.4	4.3	14.8	28.5	5.0	16.8	33.0	3.0	18.0
Nov	3.8	8.6	2.5	5.5	16.7	1.0	8.9	21.5	0.1	10.8	24.4	–2.0	11.2
Dec	–2.0	0.6	–1.8	–0.6	8.7	–3.3	2.7	13.4	–6.1	3.7	14.8	–7.4	3.7

added to the irrigated section during each week of the following months was: May, 25; June, 38; July, 50; August, 50; September, 38; and October, 25. The sprinkling regime was designed to maintain abundant grass cover on the irrigated section during the entire pasture season. The nonirrigated section received only natural precipitation.

Results

Meteorologic data.—Table 1 is a summary of the monthly meteorologic data gathered for 1976 and provides an indication of the microclimatic conditions which existed within the irrigated and nonirrigated sections of the experimental plot. All meteorologic data for the year were monitored daily and are available upon request.

As expected, irrigation greatly enhanced the favorable conditions within the microenvironment where the infective larvae of *H. contortus* were placed by markedly reducing the maximum temperatures which occurred and by increasing the moisture content within the soil. This latter factor was further reflected in the maintenance of adequate grass cover on the irrigated section for the entire study period, whereas the grass on the nonirrigated section became sparse and turned brown after the first two months of the pasture season.

During 1976 the highest monthly mean maximum temperature recorded at soil surface under grass cover on the nonirrigated section was 52.1 C during August, which compared to 26.7 C on the irrigated section. Overall, monthly mean maximum temperatures for soil surface under grass cover on the irrigated section averaged 17.7 C less than those recorded from the nonirrigated section for the months of May through October. Temperatures recorded at soil surface level from bare ground were also consistently higher on the nonirrigated section than on the irrigated section for the entire year. Monthly mean minimum temperatures recorded from the two sections were much closer than were the corresponding maximum temperatures. Monthly mean air temperatures recorded within a standard weather shelter (1.6 m above ground level) compared more closely to the monthly mean temperatures recorded at soil surface under grass cover from the irrigated section than with any of the other temperature means given in Table 1.

Figure 1 gives the pattern of precipitation for 1976, shows the amount of water added through irrigation from May through October, and depicts the comparison of soil moisture determined gravimetrically for the irrigated and nonirrigated sections. A total of only 131 mm of precipitation was received during the year, compared with the reported normal of 402 mm (Utah Agricultural Statistics 1976). With the regime used,

Moisture Pattern				Larval Recovery			
Irrigated		Nonirrigated		Irrigated		Nonirrigated	
Pptn. and water added via sprinkling (mm)	Mean percent soil moisture	Pptn. (mm)	Mean percent soil moisture	Mean no. days 0.01 percent larvae recovered	Percent larvae recovered after one week	Mean no. days 0.01 percent larvae recovered	Percent larvae recovered after one week
27.7		27.7					
14.0		14.0					
14.5		14.5					
34.4		34.4					
107.9	20.3	7.9	7.0	61	13.8	54	8.3
159.4	16.0	7.4	5.7	43	15.6	33	2.6
251.5	17.4	1.5	5.0	50	9.1	33	2.8
206.9	25.3	6.9	3.3	60	12.3	44	1.3
162.9	16.0	10.9	2.9	45	21.9	33	3.0
130.8	19.1	5.8	3.8	31	17.6	24	3.8
0.0		0.0					
0.0		0.0					

an additional amount of 979 mm of water was added to the irrigated section in the months indicated. Overall, the monthly mean of all soil moisture determinations for the irrigated section averaged 14.4 percent more than for the nonirrigated section.

Figure 2 is a bioclimatograph of monthly mean maximum temperatures vs. precipitation for the irrigated and nonirrigated sections. The double lines inside the graph represent the limits used by Gordon (1953) to indicate the environmental conditions required for optimum pasture transmission of *H. contortus*. During five of the six months of the study period, conditions on the irrigated section were within the optimum range for transmission of the parasite, whereas at no time during the year did environmental conditions measured from the nonirrigated section come within optimum limits prescribed for *H. contortus*.

Larval survival.— Twenty-six experiments were completed during this study (Figs. 3–7). The solid line on each graph represents the number of total larvae recovered at each time interval indicated from grass, soil scrapings, and remaining pellets. The dashed line represents the number of those larvae recovered from grass alone and illustrates the movement of larvae from pellets onto vegetation. Table 1 includes selected recovery data from the experiments, calculated as monthly averages for those started in each month from May through October.

In all 26 experiments, larvae placed on the irrigated section survived significantly longer (calculated from last day on which 0.01 percent of larvae could be recovered; student's *t* test for paired samples, $t = 6.53$; $P < 0.01$) than those larvae placed on the nonirrigated section (Table 1; Figs. 3–7). The longest average monthly survival for 0.01 percent of larvae placed on either irrigated or nonirrigated plots occurred for those experiments started in May (monthly average, 61 days and 54 days, respectively). Temperatures during May were moderate and the percent soil moisture for the nonirrigated section was the highest of the entire study period (Table 1).

The shortest period of time 0.01 percent of larvae survived on either irrigated or nonirrigated plots occurred for those experiments started in October (monthly average, 31 days and 24 days, respectively). October was the only month of the pasture season during which environmental conditions on the irrigated section did not fall within the limits of optimum pasture transmission for *H. contortus*.

As shown in Table 1, the average monthly recovery of larvae after seven days' exposure was also significantly greater (Student's

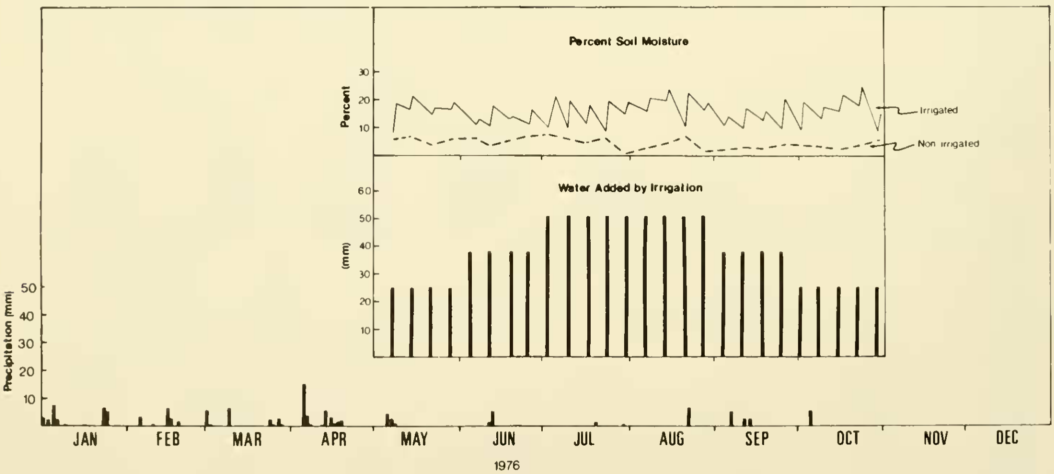

Fig. 1. Precipitation pattern, irrigation regime, and comparative soil moisture data for irrigated and nonirrigated pasture plots, Provo, Utah, 1976.

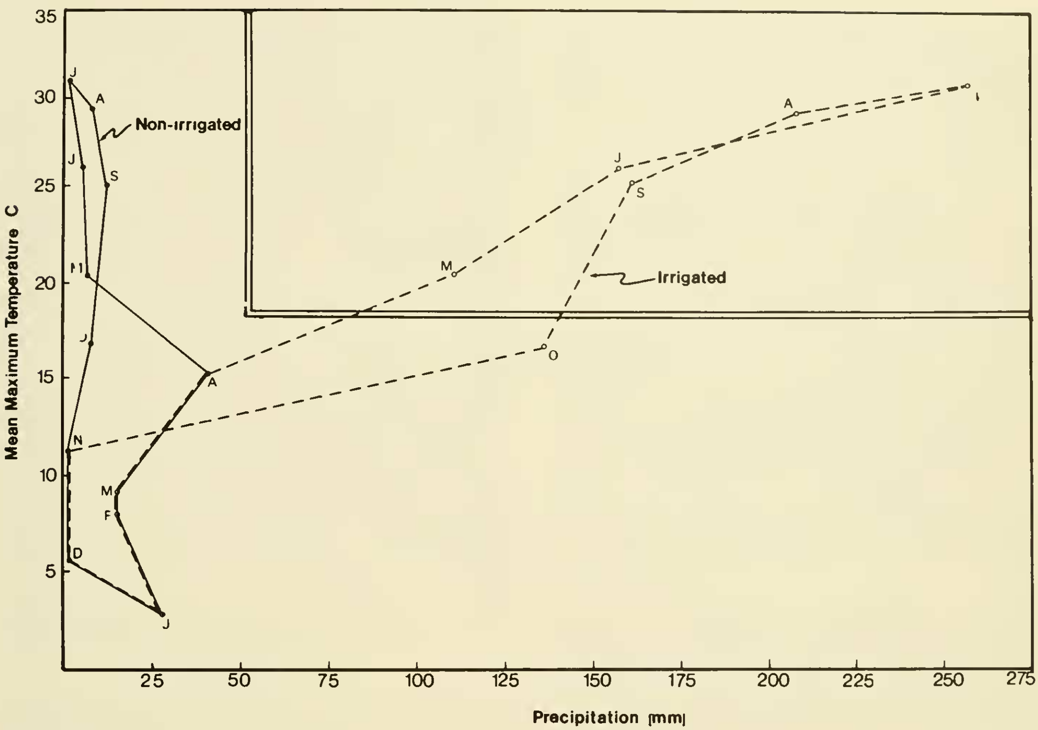

Fig. 2. Bioclimatograph of monthly mean maximum temperature vs. precipitation for irrigated and nonirrigated pasture plots, Provo, Utah, 1976.

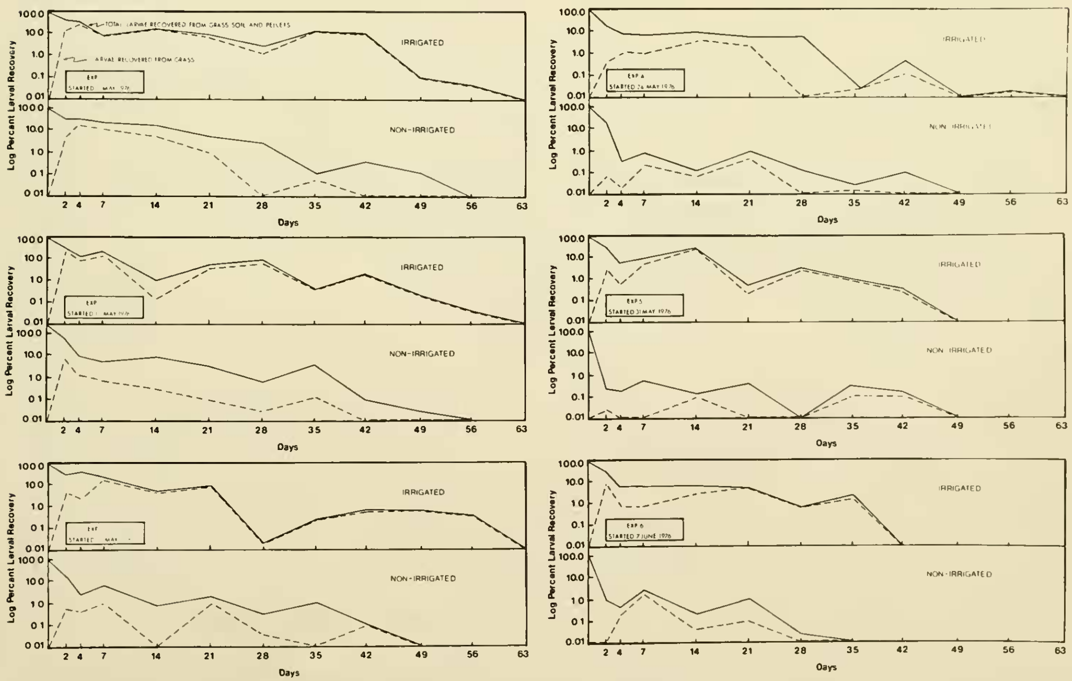

Fig. 3. Recovery of *H. contortus* third-stage larvae from irrigated and nonirrigated pasture plots, Experiments 1–6.

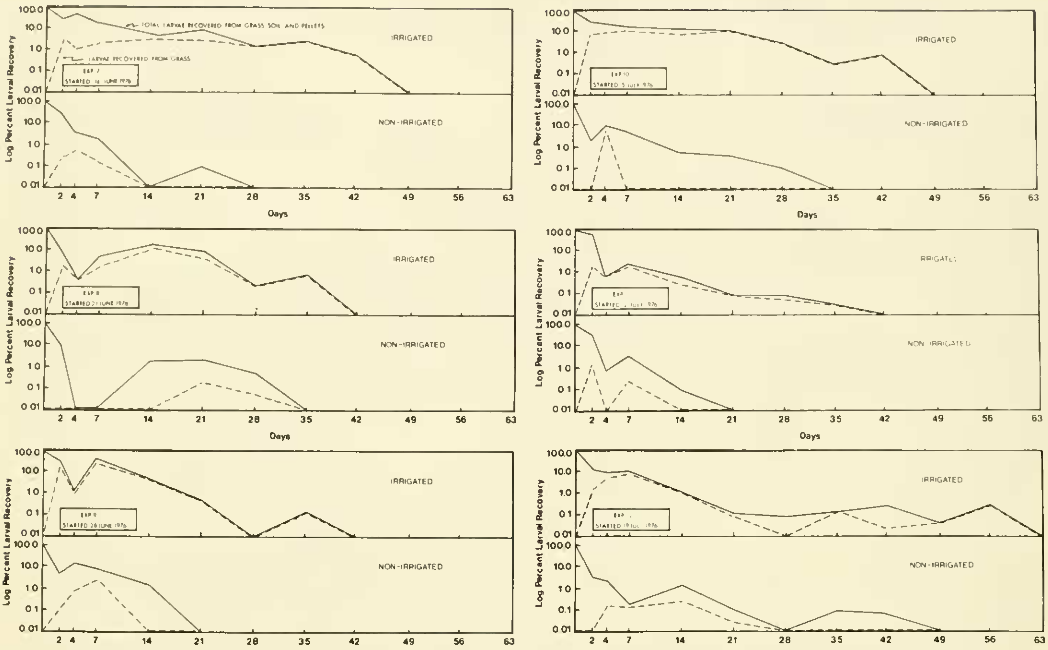

Fig. 4. Recovery of *H. contortus* third-stage larvae from irrigated and nonirrigated pasture plots, Experiments 7–12.

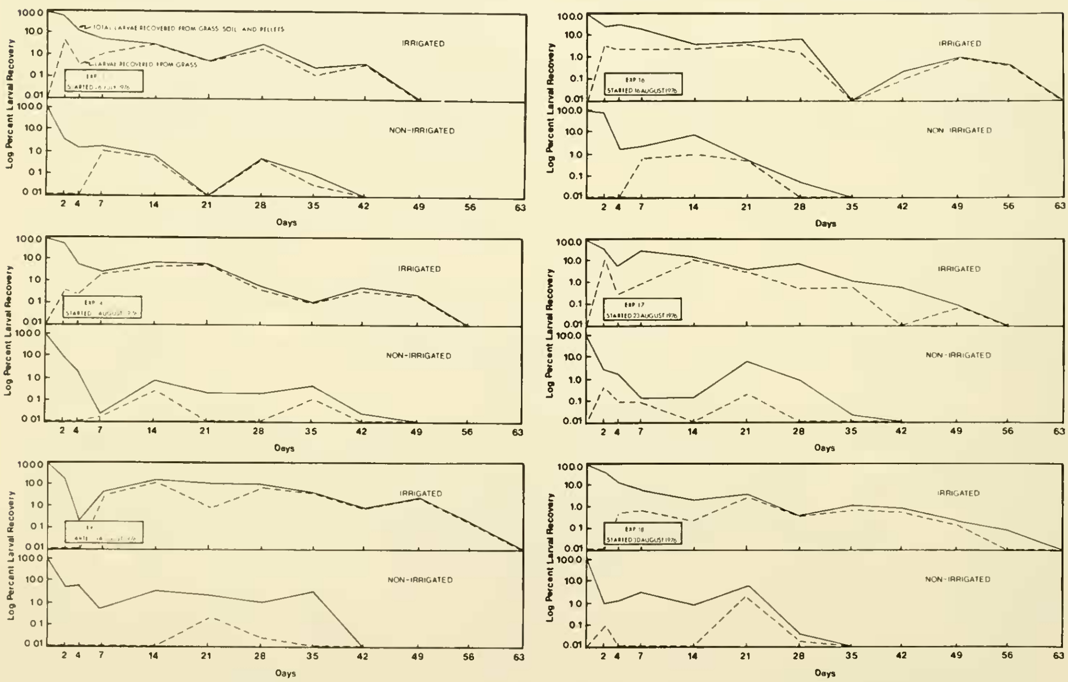

Fig. 5. Recovery of *H. contortus* third-stage larvae from irrigated and nonirrigated pasture plots, Experiments 13–18.

t test for paired samples, $t=5.58$; $P<0.01$) from the irrigated than from the nonirrigated section. The highest average recovery from the irrigated section at that time interval was from experiments started in September (21.9 percent) and lowest from experiments started in July (9.1 percent). The highest average recovery from the nonirrigated section after seven days' exposure was from experiments started in May (8.3 percent) and lowest from experiments started during August (1.3 percent).

Irrigation also appeared to affect the migratory ability of the infective larvae after the pellets had once been placed on the plots. After approximately seven days, larvae recovered from the irrigated plots were generally found in greater percentages from the glass clippings, whereas larvae recovered from the nonirrigated plots were generally found in greater percentages in the soil and remaining pellets (Figs. 3–7).

Discussion

Ecological studies on the free-living stages of trichostrongylid nematodes have been reported by such workers as Stewart and Douglas (1938), Levine (1963), Kates (1965), Andersen et al. (1970), Levine and Andersen (1973), Williams and Bilkovich (1973), Levine et al. (1974), Gibson and Everett (1976), and Todd et al. (1977). These individuals demonstrated that optimum conditions for development and/or survival differ between species of nematodes and that each particular species is limited generally to a unique climatic environment. Gordon (1953) reported that *H. contortus* flourishes in climatic regions where average monthly maximum temperatures exceed 18.3 C and where total monthly precipitation is above 50 mm. In our study, the addition of water by irrigation was sufficient to provide a total monthly water accumulation well in excess of 50 mm. Also, the resultant increase in soil moisture helped maintain microenvironmental temperatures within the optimum limits prescribed above. As a result, environmental conditions on the irrigated plots were within the range for optimum pasture transmission of *H. contortus* for five of the six

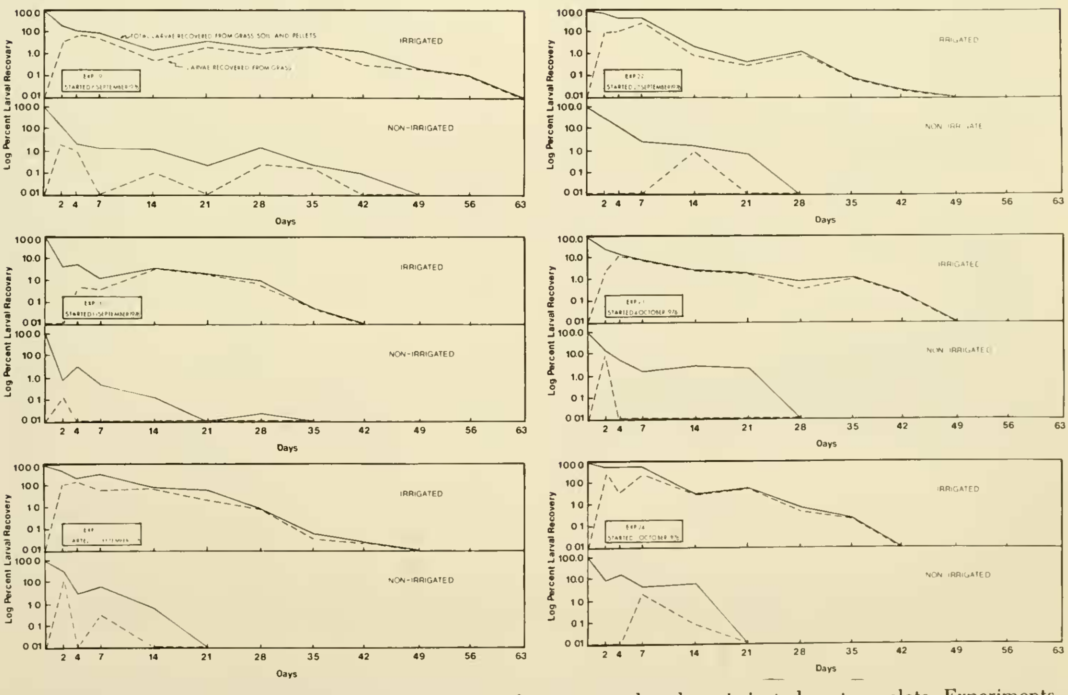

Fig. 6. Recovery of *H. contortus* third-stage larvae from irrigated and nonirrigated pasture plots, Experiments 19–24.

months of the study period. Temperatures on the nonirrigated plots, however, were usually too high for optimum larval survival and the moisture accumulation from natural precipitation alone was consistently too low.

Andersen et al. (1974) previously compared meteorologic measurements for irrigated and nonirrigated plots in the same area as the current study, and they demonstrated that the average monthly mean maximum temperatures for May through October at soil surface under grass cover for 1970, 1971, and 1972 were 23.7 and 31.1; 22.5 and 27.6; and 26.2 and 34.9 C, respectively. They further showed that the average percent soil moisture for those same months and same years from irrigated and nonirrigated plots were 16.1 and 8.4; 16.3 and 5.8; and 8.3 and 3.8 percent, respectively. The comparable figures for temperature and soil moisture content from irrigated and nonirrigated plots for the current study were 24.8 C and 19.0 percent, and 42.5 C and 4.6 percent, respectively. Some of the discrepancy from measurements taken at the same site during different years could have resulted from the fact that in the current study sprinkling irrigation was used to minimize lateral movements of the infective larvae, whereas flood irrigation was used in the 1970–72 study.

The lowering of environmental temperatures following irrigation has also been reported by such workers as DeVries and Birch (1961) in Australia, who noted a decrease during the summer of about 10 C

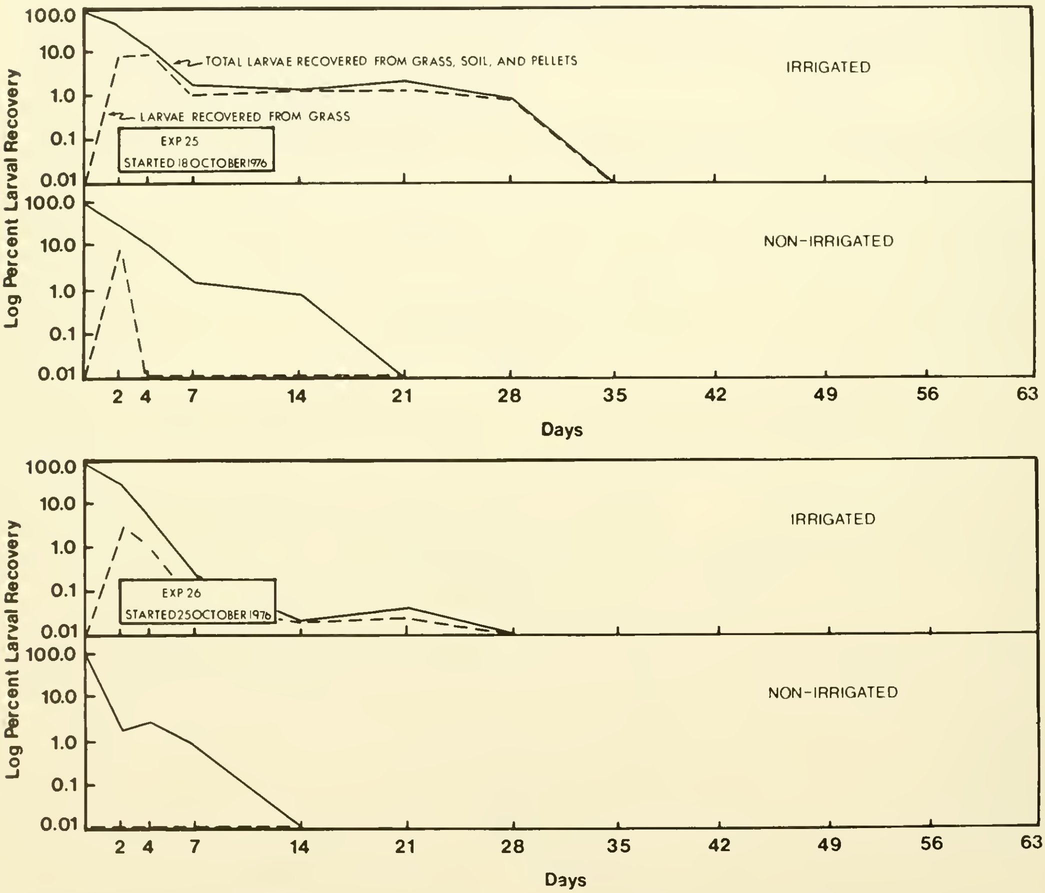

Fig. 7. Recovery of *H. contortus* third-stage larvae from irrigated and nonirrigated pasture plots, Experiments 25–26.

when the temperature was measured 5 cm below grass-covered ground, and by Leonard et al. (1971), who observed a similar decrease in an irrigated pine-covered forest in New York. Fowler and Helvey (1974) reported that air temperatures along the Columbia River Basin in Washington were well below established normals now that irrigation is so widespread in the region.

The lowering of temperatures in irrigated regions is mainly a reflection of the increased soil moisture resulting from the addition of irrigation water. Levine and Todd (1975) stated that soil moisture is a more important criterion than precipitation alone in determining optimum conditions for development and survival of *H. contortus,* since soil moisture results from an interaction of precipitation, soil type, and evapotranspiration. Soil moisture content also is the factor most responsible for the maintenance of vegetative cover. Knapp (1964) showed that different species of forage plants influenced the survival and also the infectivity of *H. contortus* in lambs. In our study, the lack of moisture on the nonirrigated section eventually killed the Kentucky bluegrass, which was subsequently replaced by a few plants with deeper tap roots. These new plants did not provide adequate cover, and soil temperatures rose drastically during ensuing months. Consequently, the pellets quickly dried and the larvae were sealed within. Andersen and Levine (1968) reported that sheep pellets routinely lose 50 percent of their original weight within 12 to 24 hr when stored at 30 C and 65 to 75 percent RH, which conditions would approximate those on our study plot. The irrigated section of the present project site maintained ample grass cover for all six months of the study period and pellets placed on the plots remained moist or disintegrated as water was added.

The number of days third-stage trichostrongylid larvae may be recovered from artificially infected pastures is not only dependent upon existing meteorologic conditions in the specific geographical location where the study occurs, but also upon the particular species of nematode studied. Gibson and Everett (1976) recovered third-stage larvae of *H. contortus* for as long as 40 weeks in England, whereas Levine et al. (1974) recovered 0.1 percent infective larvae of *H. contortus* for nine weeks in Illinois. In the present study, 0.01 percent of larvae survived on the irrigated plots for a maximum of nine weeks several times during the six-month study period and at least for a minimum of four weeks even during October, when conditions for pasture transmission were not optimum. On the nonirrigated plot, 0.01 percent of larvae were recovered for a maximum of eight weeks during May, when soil moisture content was still adequate. Thereafter, survival time dropped considerably until in October larvae were recovered for only two weeks.

In addition to an increased larval survival time on irrigated plots in the present study, an increased percentage of larvae survived on the irrigated section. Furthermore, larvae on irrigated plots were recovered almost exclusively from grass clippings after one week, whereas at that time larvae from nonirrigated plots were recovered mainly from pellets and soil scrapings. Irrigation thus aided migration of larvae from the pellets onto the vegetation, where they would be in the optimum position to be ingested by the grazing host under natural field conditions.

In summary, the present study demonstrated that irrigation enhanced the ability of *H. contortus* larvae to survive longer and in greater numbers on experimental pasture plots, and also increased their ability to migrate from pellets onto adjacent vegetation. Without suitable moisture and temperature, optimum conditions for pasture transmission would not have been achieved. Irrigational practices in Utah undoubtedly contribute to the relatively high incidence of *H. contortus* in this region where the prevailing climatic conditions indicate the parasite could not otherwise flourish.

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